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A MALE CRAYFISH WITH SOME FEMALE ORGANS

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THE crayfish to be described here was peculiar in being a male with some few of the external characters of a female. If by the term gynandromorph we understand an individual that shows both male and female organs in different parts of the body, though the normal individuals have but one set of sexual characters, we may call this crayfish a gynandromorph.

Compared with other known cases of mingled sex in the crayfishes this one is peculiar in being chiefly all male, while most of the other cases on record are predominantly female.

Before describing this crayfish it will be useful to recall that the sexual organs of crayfishes consist of the gonads, ovary and testis, their ducts, certain modified limbs to ensure the transfer of the sperm to the female from the male; and in the crayfishes of the genus *Cambarus*, a sperm receptacle upon the female in which to store up the sperm till the time the eggs are laid.

The ovary of the female is a median mass that becomes filled by the large eggs and from it an oviduct passes down on each side of the body to open out upon the base of the antepenultimate leg, right and left, as a rounded hole that is closed by an operculum, except at the time of egg laying.

The testis of the male is a similar but smaller body from which a convoluted duct leads down each side to open out on the base of the ultimate leg at the tip of a perceptible papilla which is turgid with the pressure of the blood.

The limbs of the female are reduced, or absent, upon the

first somite of the abdomen, while those on the second are like the following ones. But the limbs on the first somite of the abdomen of the male are quite remarkable conduits that conduct the sperm; and the limbs of the second somite are peculiarly adapted to fit against the first as a necessary part of this sperm-transferring apparatus. The limbs of the thorax may also be modified so that some of them bear hooks for holding the female.

In the case of *Cambarus* the female sperm-receptacle is a unique median pocket in the shell, which is of as much physiological necessity for the race as are the ovary, the testis and the male appendages that transfer the sperm.

The gynandromorphic crayfish to be described was a small sized and probably immature male of the species *Cambarus affinis*, taken in a lake at East Hampton, Conn., by Mr. Kenneth N. Atkins.¹

The external appearance of this specimen was that of a male 55 mm. long with small chelæ only 30 mm. long, having the hand 15 mm. long and 5 mm. deep. The antennæ were 45 mm. long. The papillæ of the fifth or ultimate legs seemed normal. The second abdominal limbs were as usual in a male but the first were of the puerile or so-called second form of male limb very like that found in a young normal male five months old and 38 mm. long. The tips were blunt and there was a free joint above the basal joint. The attaching hooks of the third, or antepenultimate, legs were short and blunt, but normal for the young male. There were the usual long male hairs on the spine between the ultimate legs, and

¹ The finding of this species in this locality is of interest as bearing upon the geographical distribution of crayfishes. New England being singular in the fewness of its crayfishes, which are largely restricted to the drainage into the St. Lawrence, the question to be settled is whether the crayfishes are absent because they never got there or because some characteristics of climate, soil or biological environment are inimical to them. It seems that these crayfishes were first observed in this lake some nine years ago, being, it is thought, brought there by fishermen. Since these crayfish are fairly abundant there now this is evidence that crayfish can live in this region, and favorable to the idea that the relative absence of crayfishes throughout these states is due to their not having migrated in there.

no sign of any female organ, the sperm receptacle, anterior to it.

To these male external features there were added the two female openings on the antepenultimate legs. On the right the basal segment of the leg bore a well-formed normal female orifice, that is, a soft, round, depressable area, or operculum. This opened along the median edge as a curved mouth bounded by a narrow stiff rim of hard shell. On the left the opercular area was perhaps somewhat less perfect, its median side being more a straight line which opened as a mouth, and the curved bounds were more vague. The hard rim was thicker, apparently by the amount that the straight mouth should have been curved to make the normal contour.

On dissection the internal organs were found to be entirely those of a male, for the above female openings had no connection with the interior and there were no oviducts nor ovaries. On the right the operculum, when pushed in, showed a short conical pocket that received a needle point but appeared to end blindly as a mere thin chitinous continuation of the shell inwards. This pocket was flat. The mouth was a little more than 1 mm. long and the pocket slightly shorter than the mouth, on the right side. On the left the mouth slit led into a pocket of less extent.

The essential internal organs of this animal were the testis and the two efferent ducts. The testis was a median mass some 3 mm. long under the heart, with two anterior lobes about 2 mm. long rising upwards in front of the heart. Besides this well-developed part the testis was continued back over the intestine as a short minute membranous thread and forward between the stomach and the hepato-pancreas as a clear tubular membrane, or sterile part of the testis about 2 mm long, from the right and from the left lobe.

Where the right and left lobes joined the median lobe the different duct sprang out each side and, passing back alongside of the median lobe some 3 mm., went away at

right angles over the surface of the dorsal muscle-mass that comes into the thorax from the abdomen on the side of the thorax, without any coils or turns, some 4 mm. Each duct then descended in a slightly sinuous course to the projecting base to which the antepenultimate leg is attached, where it became thicker and, making a short semicircular curve, entered the basal joint of the leg and passed straight out to the tip of the papilla. The duct contained sperm.

Comparing these findings with the anatomy of normal young males and females of the same species, we see that in a male of 65 mm. killed in October the first pair of limbs on the abdomen have much more perfected tips and lack the joint near the base; while internally the sperm ducts that lie alongside of the median part of the testis are so coiled as to be there about 20 mm. long instead of 4 mm. The duct was also larger and contained more sperm. Allowing for the differences in size and in time of year, the two specimens are essentially alike and we may regard the abnormal one as perfect in all its male organs, though they had not reached their final form. Doubtless this male would have been able to transfer its sperm to a female in the proper season, that is, in the fall.

Serial sections of the testis show no indications of any hermaphrodite nature, no ovogenesis in any part. On the other hand, the different duct and the collecting tubules contain some nearly mature sperms. Some of the acini show spermatogonia with equatorial plates.

The two sham oviduct-openings of this specimen when compared with the real openings of a female of October, some 60 mm. long, show the closest agreement externally. But there is the fundamental difference internally that the normal mouth, instead of leading into a blind, minute pocket, continues directly as a wide and comparatively straight tube some 10 mm. upwards to the ovary.

In brief, then, this gynandromorph was a young male that would have functioned as such at the next breeding season, yet it presented two female characters, openings

as if to lead to ovaries, but with no internal connections and no discoverable use. These sham openings stand in the proper place for the oviduct openings of a female.

A review of the literature fails to show any abnormal crayfish with just these combinations of male and female characters; in fact, as before stated, most of the known cases are females with some male features. Recorded abnormalities of crayfishes include the cases of repetition of parts in one sex and the cases of mixtures of traits of two sexes. The former have been brought together by Bateson in "Materials for the Study of Variation," Macmillan, 1894, the latter by Hay in "Instances of Hermaphroditism in Crayfishes," Smithsonian Miscellaneous Collections, 1905.

In his monograph on the crayfishes of Pennsylvania Ortmann has recently described five additional cases in *Cambarus*, in which the external sex organs are more or less mixed and in part defective.

Bateson found that in 586 females of *Astacus fluviatilis* there were 23 abnormal cases. In these, besides the usual openings upon the bases of antepenultimate legs, there were one or two similar openings upon the penultimate, the ultimate or even upon all; making a maximum of three pairs of openings. Moreover, the oviducts generally branched so that more than one pair of oviduct openings might be functional, but in other cases the extra openings might end blindly and be of no use. Of 714 males only one was abnormal and that presented not a duplication, but a suppression of organs, having no trace of a generative opening upon the right side, while the sperm duct of that side hung blindly in the body cavity.

A real case of duplication of sexual characters in a male crayfish was recorded, in a rather inaccessible publication, the *Indiana University Bulletin*, by W. J. Moenkhaus, in 1903. He found in *Cambarus viridis* a male that had in addition to the usual first and second male limbs of the abdomen the third pair modified to exactly resemble the

second, in plan, and to differ from them but slightly in the detail with which this was carried out.

These cases of duplication of external organs must not be confounded with the gynandromorph here described since that has both male openings and female openings and not a mere duplication of the openings of one sex. There is so much difference between the male papillæ of the fifth legs and the operculate openings of the antepenultimate legs of the female that we must regard them as two morphologically and physiologically distinct organs and their occurrence upon the same animal is not the same thing as the duplication of one set upon one animal. This is true even if there were reason to suppose that both kinds of openings may have had some common origin in the past.

The cases of hermaphrodite crayfishes previously on record were considered by Hay along with most interesting new cases. It appears from his paper that there are in crayfishes no known cases of such complete, typical, gynandromorphs as that of the lobster described in 1703 as having both external and internal organs of the male on the left side of the body and of the female on the right. All crayfish gynandromorphs, but one, are really either males or else females as regards the gonads, and have added but some of the external organs of the opposite sex. One is a female with a little testis as well as external organs of the male.

The numerous cases of crayfishes from the southern hemisphere with the external openings of both males and females described by different authors are especially interesting as resembling the gynandromorph of this present paper, since it was found by Lönnberg,² that whenever the internal anatomy was made out, the animal had either a testis or an ovary, and if there was a testis the normal ducts led to the normal male openings, while the redundant female openings had no internal connections, though the testis did send out an extra duct towards the

² *Zool. Anz.*, 1898.

pseudo-female opening; while if there was an ovary the oviducts went to the normal openings and the extra male openings were of no use, though here again the ovary sent out a duct towards the useless male openings.

The extra openings, however, Lönnberg found to be shams, or closed openings, yet they look like the openings of the opposite sex.

This state of things, the perfect male or female with sham openings and pseudo-ducts of the opposite sex, seems to be the usual, if not the only, condition found in many species of the genus *Parastacus*, to judge from all the specimens that have been studied. The relationship between *Parastacus* and *Cambarus* is, however, believed to be so very remote that one can not suppose the present case of abnormality in a species of *Cambarus* has any genetic connection with what seems to be the rule in many, but not all, species of *Parastacus*.

The other recorded gynandromorphs are one specimen of *Astacus* and fourteen of *Cambarus*, and all except one are females that have some male characters added. The superfluous male characters are sometimes but the modification of the first abdominal limbs to resemble those of the female, in others both these and the following limbs are just like the male limbs. In one the male attachment hooks, and the male openings and even the hirsute spine posterior to the somite of the sperm receptacle, that is, all the external characters of the male, are present along with normal ovary and oviduct.

This last was the most hermaphroditic of all known crayfishes. It was the female *Cambarus affinis*, 106 mm. long, described by Hay. This seemed externally a male and attempted conjugation with a female, having a good set of male external organs. But internally it had a large ovary with nearly mature eggs and two perfect oviducts. The specimen was thus deficient in lacking the sperm receptacle that a female of this kind of crayfish should have in order to get the eggs fertilized. In addition to the ovary there was a small testis, on the right,

with a duct leading to a single male opening on the ultimate leg. Though no sperm was present it seemed as if sperm might have been made. It appears that this individual could have been of little or no use to the race.

With this exception all sexually abnormal crayfishes, as far as known, are either males or females with either some duplication of organs that belong to that one sex or else the addition of external organs of the opposite sex. But in *Parastacus* there is also some duplication of internal ducts, which needs additional investigation to show how far it is duplication and how far it may be the addition of ducts of the other sex. As far as Lönnberg's observations go the extra ducts were like the normal of that sex and not like those of the other sex.

The fact that the male may have merely the external openings of the female sex without any internal female organs shows that the gonad is not necessary as a stimulus for the making of the external organ, that the external organ is not correlated with the gonad by any internal secretion or other means, necessarily. At the same time *Parastacus* shows that when there are extra openings, or rather sham openings, the gonad sends extra ducts towards those openings so that there seems a correlation between the gonad and the external organ that belongs to the opposite sex. However, Lönnberg found in some of the testes of *Parastacus* objects that he thought might be eggs; so that the purity of the gonads is somewhat doubtful.

There is a possibility that these males may have had enough development of a hermaphrodite gonad to supply a stimulus to the surface that would make the external female organs begin to develop in the right place for a female having ovaries, though the gonad was essentially male.

The gonads of crayfishes are late in becoming visible in the ontogeny of the individual and the external organs do not show till the eggs have hatched and passed into the third larval stage, after two moults. Whether these

external organs would develop at all without the internal gonad can only be determined by future experiment, but the abnormal cases above cited show that the external organ may be formed without the gonad of that sex to which the external organ ought to belong and make it probable that the external organs and the gonads are so independent that we need not suppose one leads to the formation of the other.

The sex of the crayfish is not merely the possession of egg or sperm, but of something made evident in a variety of places over the body, as sex organs that are accompanied by the necessary reflexes and instincts to use them.

That the sex is rather intimately dependent upon function seems to be indicated by the occurrence of the two forms of male, known as the first and second, which alternate in such a way that at the breeding season the external organs of the male are perfect, while at another time of year the same male has relapsed into a juvenile state in which the sperm transfer organs are as they were in youth and probably of little or no functional value. These morphological changes are made possible by the shedding of the shell and the growth of what is practically a new organ.

We have then some reason for supposing that back of the visible sex organs there is some state or condition of the organism that can at least modify the structure of the sex organs.

Nothing is known as to the origin of these gynandromorph crayfishes. But regarding the eggs as at first able to make either male or female, or make more than one individual under certain circumstances, the gynandromorph may be looked at as a partial realization of the entire set of possible organs. The causes may lie in physiological states present at various stages of ontogeny. Where a whole species is gynandromorphic the egg may be predestined in the ovary to produce a mixture of organs. When only an occasional individual has

a few external organs added to the normal set the causes may lie in conditions not found till late, after fertilization.

Just as the determination of sex may be due to different conditions in various animals and plants, so the repression or the expression of one or another sex organ may be due to diverse causes acting at various periods of ontogeny, and not to any single factor. Moreover, we do not know how far the gynandromorph may be the result of aberrations independent of the causes of determination of the gonads.

However amongst the insects, where gynandromorphs are well known, there are reasons for restricting our surmises as to the time of origin of the mixed expression of sex organs. Here the mixing seems to be associated with the period of fertilization. In the honey bee the sex is determined, apparently, in fertilization and the phenomenal cases of gynandromorphs, such as those studied by V. Siebold in 1863, in the Eugster hive, have often been explained as due to abnormal fertilizations. This interpretation has been most acutely elaborated by T. H. Morgan on the basis of the facts of experiments upon echinoderms and the results of Toyama upon hybrid moths. He is finally led to the view³ that the egg nucleus by itself would produce male, the sperm nucleus by itself also male, but the two combined produce female. The gynandromorph would be the result of polyspermy. It would be a sort of combination of individuals, the one female, arising from the part of the egg containing the fused egg and sperm nucleus; the other, male, arising from the part of the egg in which extra sperms developed without contact with the egg nucleus. The female parts of the gynandromorph would have two parents and should be mixed in a hybrid, the male parts would have but one parent and should be pure in a hybrid.

The hypothesis of polyspermic origin of gynandromorphs might be applied to the crayfish with the common assumption of two sorts of sperm, male producing and

³ This journal, November, 1907.

female producing.⁴ We assume that every egg is fertilized and will be male or female according to the sperm that unites with its nucleus. But a gynandromorph might arise by adding to the male or the female some organs of the opposite sex due to the independent development of the opposite kind of sperm in parts of the egg. All sorts of gynandromorphs might be imagined upon this basis. Moreover, we might assume the abnormal cases of duplication of sex organs in one individual, such as studied by Bateson, to be due to the independent development of sperms that happened to be of the same kind as the one that fused with the egg nucleus. In theory we might even refer the doubleness of organs not concerned with sex to some sort of super-fertilization.

Whether such hypotheses have any value may be determined by future experiments in the cross breeding of crayfish. Such experiments may enable us to decide whether gynandromorphs arise before, during or after fertilization and may throw light upon their causation. The crayfishes in this part of the world, are especially well adapted to these experiments, for if crosses can be obtained at all, we may expect to distinguish between pure and mixed sex organs, since both the male and the female have external organs that are at the same time essential sex organs and characteristic specific characters.

Meanwhile the totality of facts known seems to mean that the gynandromorph crayfishes are caused by unknown disturbances, which may happen at various periods of ontogeny, though probably more often in the ovarian egg; that these disturbances may have no connection with the gonads; and that if in some cases the disturbances are possibly associated with polyspermy, in general they seem more fundamental and deep seated amidst the causes of symmetrical form within the egg.

BALTIMORE,

January 11, 1909.

⁴In some crayfish there are visibly different forms, some are wound clockwise and some counter clock, some have more and others less rays.